

ILLUSTRATIONS OF  
NORTH AMERICAN  
PITCHERPLANTS

*BY*

MARY VAUX WALCOTT

## DESCRIPTIONS AND NOTES ON DISTRIBUTION

By EDGAR T. WHERRY

## NOTES ON INSECT ASSOCIATES

By FRANK MORTON JONES

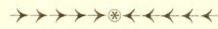


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## FOREWORD

THE STUDENT of wildflowers encounters many forms that are of unusual interest for one reason or another, but next to the orchids, probably the most spectacular are the members of the family of pitcherplants, comprising only fifteen species in the United States and Canada. Their beautiful coloring and strange mode of growth alone would make them outstanding among wildflowers; add to this the amazing association with insect life, wherein insects are trapped in the pitchers and digested by the plants, and their strong appeal to the curiosity and interest is easy to understand.

The collection of pitcherplant sketches here gathered together is the result of several years' work. Eight of them were published in the writer's "North American Wild Flowers"; these, with the others, mostly new forms recently collected, comprise all the known members of the family that are native in North America. All occur east of the Rocky Mountains, except the California pitcherplant, native in northern California and southern Oregon. Four species are known from Guiana.

The plants grow in acid soil in peat bogs and savannahs, mainly along the Atlantic Coastal Plain at low altitudes. They range from the southern United States bordering the Gulf of Mexico and in the lower Mississippi Valley and northward up the Atlantic Coast into Labrador. In Canada they are found as far west as the Athabasca valley.

With proper care most of them can easily be grown in a cool green-

house. They should be planted in a mixture of peat and sand in a pot placed within another pot of two inches greater diameter. The space between should be filled with sphagnum moss, which must be kept moist. Rainwater or other soft water should be used.

The illustrations show the striking coloration of the flowers of the various species of pitcherplants. The petals of some of the varieties last but a short time, but after they drop off, the curious umbrellas which are left on the stem are in some species also brilliantly colored. The fascinating mechanism of the pitchers, or insect traps, are described in detail in Dr. Jones' article which forms a part of this publication, but to illustrate the unusual features of these plants I may mention one strange adaptation. In the hooded pitcherplant, the pitchers are darkened by their arching tops, and to introduce sufficient light to entice insects into the pitchers, the yellow-green tissue of the walls contains a number of white translucent patches which serve as windows.

Many of the plants were brought into bloom by Dr. Frederick V. Coville in the greenhouses of the Department of Agriculture in Washington. To him, and to Dr. Wherry and Dr. Jones, who have contributed the articles on specific phases of the study of pitcherplants, I extend my sincere thanks, as I do also to those other friends who have gathered the specimens that I have sketched.

MARY VAUX WALCOTT









## CALIFORNIA PITCHERPLANT

*Chrysamphora californica* (Torrey) Greene

Although California pitcherplant is often called *Darlingtonia*, that name is not acceptable under the standard rules of botanical nomenclature, since it had previously been used for an entirely different plant. The name suggested by Greene to replace it, *Chrysamphora*, comes from the Greek words for "golden pitcher." The genus, which comprises but a single species, was discovered in 1842, near Mount Shasta, California, by members of the Wilkes Exploring Expedition.

Nectar is secreted on the concave upper surface of the fishtail-shaped appendage of the pitcherleaf, and insects alight there to feed upon it. Following along the curving channel, they unwittingly enter the orifice and fall to the bottom of the hollow. Their contact with the walls stimulates the secretion of water, in which they are drowned. So far as known, this pitcherplant produces no digestive ferment but obtains its nourishment from the materials liberated by bacterial decomposition of the dead insects.

The plant sketched came from the mountains of northern California, where the species is locally abundant.









## GREEN PITCHERPLANT

*Sarracenia oreophila* (Kearney) Wherry

So far as known, green pitcherplant was first collected about 1875 by Dr. H. M. Neisler in Taylor County, Georgia. He recognized that it differed from the widespread *Sarracenia flava* in that it develops short, flat leaves in addition to the hollow pitchers, and also in the absence of disagreeable odor from its flowers. Specimens were sent to Asa Gray and to John Torrey for naming, but they minimized the differences and failed to consider its possible distinctness. Botanists who found it subsequently in the mountains of Alabama classed it as a variety or relative of *Sarracenia flava*. That it deserves full species rank was pointed out by Dr. Edgar T. Wherry in 1933.

The presence of flat leaves and the greenish color of the petals show it to be a primitive pitcherplant, and it may represent the ancestor of all the others.

Clumps collected by Dr. Wherry in 1932 near Center, Cherokee County, Alabama, were brought into bloom the following spring in the greenhouses of Louis Burk at Latham Park near Philadelphia. The sketch here reproduced was made from one of these.









## PALE PITCHERPLANT

*Sarracenia sledgei* Macfarlane

Although collected by Drummond in Louisiana as early as 1832, pale pitcherplant was not correctly interpreted for more than seventy years. At first it was confused with *Sarracenia flava*, a species that occurs farther east, and later it was thought to represent one that had been collected by Elliott in South Carolina and named *Sarracenia catesbaei*. Then, in 1904, Dr. J. M. Macfarlane discovered that the plant to which Elliott had applied the latter name represented a hybrid between two species, so that a new name was needed for the pale pitcherplant. Finally, in 1907, Macfarlane named it *Sarracenia sledgei* in honor of Dr. W. H. Sledge, of Mobile, who had sent him specimens and living plants to enable him to study and describe its features.

Although closely related to, and presumably a direct descendant of, the green pitcherplant, the present species differs in the absence of short flat leaves and in the greater delicacy and creamy color of the petals. The specimen sketched was grown in the United States Department of Agriculture greenhouses by Dr. Frederick V. Coville from roots sent from Mobile, Alabama.











## YELLOW PITCHERPLANT (Trumpetleaf)

*Sarracenia flava* Linnaeus

The conspicuous yellow pitcherplant was probably seen by many early explorers of the southeastern United States, but it was first fully described by Catesby in 1731 under the name "Sarracena foliis longioribus & angustioribus". Although his figure was rather crudely drawn and has been thought by some to represent other species nevertheless it agrees in all essential respects with the yellow pitcherplant. In assigning binomials to all known plants in 1753, Linnaeus selected the color as its most characteristic feature and accordingly named it *Sarracenia flava*.

Like the pale pitcherplant, the present species is to be regarded as a descendant of the green pitcherplant of the Alabama mountains. It differs in having conspicuously reflexed hood margins and decidedly ill-scented flowers with large, delicate, bright yellow petals. Its foliage varies considerably in coloring, being often veined or blotched with purple. In the specimen here figured, however, the purple pigmentation was developed scarcely at all. It was grown by Dr. Coville in the Department of Agriculture greenhouses from roots received from North Carolina.









## RED PITCHERPLANT

*Sarracenia jonesii* Wherry

The red pitcherplant was for many years confused with other species. It was first collected, about 1850, by Rugel in the North Carolina mountains, but because of its red flowers was assumed to represent *Sarracenia rubra* Walter. In 1929 Dr. Wherry pointed out its distinctness from that plant and named it in honor of Dr. Frank Morton Jones, who had carried on important studies on the relations of insects to pitcherplants.

The pitchers of the present species are so similar in size and shape to those of the green pitcherplant that there can be no doubt of the close relationship of the two. They differ, however, in flower characters, the one here under discussion being sweet-scented and having large petals of an intense red color, features that represent a decided evolutionary advance.

After the distinctness of this plant was recognized, Dr. Coville obtained roots from the North Carolina mountains and grew it in the Department of Agriculture greenhouses.









## WHITETOP PITCHERPLANT

(Drummond Pitcherplant)

*Sarracenia drummondii* Croom

Whitetop pitcherplant, the most striking of all the eastern species, was apparently discovered by William Bartram in 1775, but he failed to describe it correctly, having confused two species. It was again found by the French explorer Robin and was regarded by him as a species of *Arum*. Recognizing its true relationship, Rafinesque named it *Sarracenia leucophylla*, and this name has priority over that assigned to it by Croom. Because Rafinesque's description was inadequate, however, most botanists use the later name.

The flowers of this species are similar to those of *Sarracenia jonesii*, presumably its ancestor, although the red coloration is even more intense. Further evolutionary advance is shown by the leaves, which are taller and, when more mature, more brilliantly colored. The hood and upper part of the tube are white, with broad veins that are green when the leaf first develops, but later turn more or less red.

The illustration represents a specimen grown by Dr. Coville from roots sent from Alabama.







## SWEET PITCHERPLANT

*Sarracenia rubra* Walter

One of the pitcherplants discovered by Walter and first described in his *Flora Caroliniana* in 1788 was the inconspicuous sweet pitcherplant. Not only are its leaves and flowers smaller than those of most other members of the genus, but it is also more delicate and more easily injured by external influences such as late frost, severe drought, and attacks by parasites. There is, however, one attractive feature in which it surpasses all the others, namely, the exceedingly sweet odor of its flowers, to which the common name refers. This fragrance closely resembles that of grape blossoms, but also suggests crushed raspberries.

This species, like the whitetop pitcherplant, shows evidence of being a descendant of *Sarracenia jonesii*, but the changes were in the opposite direction. Instead of an increase in stature and in complexity of color pattern, the present species shows diminution in these respects, and its fragrance seems to be the only feature in which it excels its presumable ancestor.

The specimen painted was grown in the Department of Agriculture greenhouses, having originally come from South Carolina.









## HOODED PITCHERPLANT

*Sarracenia minor* Walter

The hooded pitcherplant was first described by Walter in 1788 and given the name here used. Michaux discovered it independently, and named it *Sarracenia variolaris*, but as this name was published some years later, the rules require its rejection. It varies greatly in stature, being sometimes but a few inches in height, when the name *minor* is appropriate. In most of the plants the pitchers reach a length of one to two feet, but in the Okefinokee Swamp in southern Georgia a variety or related species grows to a height of nearly four feet.

The yellow petal color suggests that this species is a direct descendant of *Sarracenia oreophila*, although the arching hood that excludes rain water and the translucent membranes that permit light to enter the pitcher represent evolutionary advances, indicating the former existence of intermediates which have since become extinct.

This species does not thrive as well as some of the others under greenhouse conditions. The sketch was made from plants collected near Beaufort, South Carolina.









## PARROT PITCHERPLANT

*Sarracenia psittacina* Michaux

The diminutive parrot pitcherplant is reported to have been observed as early as 1766, but was not described until 1803. Michaux stated that it occurred southward from Augusta, Georgia, but in recent years it has not been found within fifty miles of that city.

The peculiar features of this species may well have originated from the continued operation of the evolutionary trends which led to the development of *Sarracenia minor* from a primitive ancestor. The down-arching of the hood over the pitcher continued to the point of union with the walls, leaving only a small lateral orifice. The pitchers shifted to a decumbent position, enabling water to enter them during flooding of the meadows in which the plant grows. The flower parts became suffused with red pigment, although the petals still exhibit an underlying yellow hue like that of the presumable ancestor, the hooded pitcherplant.

The specimen sketched was grown in the greenhouses of the Department of Agriculture in Washington.









## SOUTHERN PITCHERPLANT

*Sarracenia purpurea venosa* (Rafinesque) Wherry

Specimens of southern pitcherplant must have been sent to England in early Colonial times, for it was figured by Plukenet in 1705 under the name "Bucanephyllon americanum." The first colored plate of it was published by Catesby in 1731. Linnaeus failed to separate it from its more northern relative, and in his *Species Plantarum* of 1753 he grouped them together under *Sarracenia purpurea*. In 1840 Rafinesque recognized its distinctness, and named it "Sarazina venosa." It intergrades too much with the northern pitcherplant to be maintained as a distinct species, however, and in 1933 Dr. Wherry classified it as a subspecies, under the name heading this page. It differs from its northern relative in having a broader pitcher with more ample hood, often pubescent on the outside, and paler petals, ranging in color from light red to rose-pink.

Roots of the southern pitcherplant were sent to the Department of Agriculture greenhouses from North Carolina in 1931, and the painting here reproduced was made from one of these when it came into bloom a few weeks later.











## NORTHERN PITCHERPLANT

*Sarracenia purpurea gibbosa* (Rafinesque) Wherry

One of the earliest known figures of a *Sarracenia*, that published by Clusius in *Historia Plantarum Rariorum* in 1601, represented this subspecies. Linnaeus did not distinguish it from the southern one, but Rafinesque in 1840 named it "Sarazina gibbosa". Reasons for interpreting it as a subspecies were published by Dr. Wherry in 1933. Its pitchers are relatively long and narrow, with a rather small hood behind the orifice, and pubescence only rarely appears on the outer surface. The petal color is usually of an intense deep red, but a mutation in which the whole plant lacks red pigment, and of which the petals are bright yellow, appears occasionally. This was named *Sarracenia heterophylla* by Eaton, but is now regarded as deserving at most only the status of a form.

A related plant, characterized by the presence of elongated rhizomes, has recently been named *Sarracenia purpurea stolonifera* by Drs. John M. Macfarlane and D. Walter Steckbeck. It does not differ from the others in leaves or flowers sufficiently to be included here.

The specimen sketched came from the bogs of eastern Maryland.









## CATESBY PITCHERPLANT

× *Sarracenia catesbaei* Elliott

Most of the species of *Sarracenia* discussed in this publication are capable of hybridizing with one another, and the hybrids combine the characters of the parents in a striking way. The cross most frequently found in nature is that of *Sarracenia flava* and *S. purpurea venosa*, with leaves and petals intermediate in shape and coloring between the two. For many years this was supposed to be a distinct species, and it was named by Elliott in honor of Catesby, who published the first colored plates of pitcherplants, but its true nature was pointed out by Macfarlane in 1904.

The specimen sketched came originally from Quincy, Florida, and was grown for a number of years in the Department of Agriculture greenhouses.







*Sarracenia drummondii* × *rubra*

This hybrid was produced by Dr. Frederick V. Coville in the Department of Agriculture greenhouses, the plant having reached blooming size from seed in three years. In leaf and flower characters it lies midway between its parents. Some of the plants produce flowers having the large size and rich coloring of *Sarracenia drummondii*, with a sweet odor derived from the other parent, *Sarracenia rubra*.









*Sarracenia rubra* × *purpurea venosa*

This is another wild hybrid, which combines the characters of its parents in a striking way. It was collected in southeastern North Carolina by Sir Henry Wellcome, and presented by him to the United States Department of Agriculture.









*Sarracenia minor* × *psittacina*

This represents a natural hybrid, collected by Dr. Wherry in southern Georgia, where it grew in company with its parents. The leaf orifice is intermediate in size between those of the two parent plants, and the petal color shows a combination of the yellow of the first with the red of the second species.









# DISTRIBUTION OF THE NORTH AMERICAN PITCHERPLANTS

BY EDGAR T. WHERRY

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The pitcherplant family (*Sarraceniaceae*) consists of three genera, *Sarracenia*, *Chrysamphora*, and *Heliamphora*. Nine species of *Sarracenia* have been recognized thus far, one of them ranging from the Gulf Coast far north into Canada, the others restricted to the southeastern United States. The genus *Chrysamphora*, also known as *Darlingtonia*, is monotypic, its single species occurring in northern California and southwestern Oregon. One species of *Heliamphora* was described in 1840 and for ninety years remained the only known representative of the genus, but three more have now been found. These are limited to northern South America, however, and will not be discussed in this article.

## KEY TO THE NORTH AMERICAN PITCHERPLANTS

- Pitcher hood bearing a fishtail-shaped appendage; scape bracted; petals bronzy yellow; style radiate . . . . . *Chrysamphora californica*
- Pitcher hood not appendaged; scape naked; style normally expanded into an umbrella-shaped structure . . . . . *Sarracenia*
- Pitchers erect or essentially so.
  - Pitcher orifice incompletely covered by hood.
    - Margins of the large hood more or less reflexed.
      - Hood yellow-green, veined or suffused with red.
        - Petal-color of a yellow type.
          - Reflexing of hood margins slight; petal texture firm.
            - Flat leaves abundant; petals greenish yellow . . . . . *S. oreophila*
            - Flat leaves sparse; petals creamy yellow . . . . . *S. sledgei*
            - Reflexing conspicuous; petals delicate, yellow . . . . . *S. flava*
          - Petal-color of a red type . . . . . *S. jonesii*
        - Hood white, green- and red-veined; petals red . . . . . *S. drummondii*
      - Margins of the small hood not reflexed; petals red . . . . . *S. rubra*
    - Pitcher orifice well covered by hood; petals yellow . . . . . *S. minor*
  - Pitchers decumbent; petals red or exceptionally yellow.
    - Orifice lateral, small; hood closed . . . . . *S. psittacina*
    - Orifice terminal, large; hood open.
      - Pitcher outline short and broad . . . . . *S. purpurea venosa*
      - Pitcher outline long and narrow . . . . . *S. purpurea gibbosa*

Data as to the relationships and distribution of the species have been obtained mainly from studies in the herbaria of the Academy of Natural Sciences of Philadelphia, Canadian National Museum, Cornell University, Gray Herbarium, New York Botanical Garden,

United States National Museum, and University of Pennsylvania, and from the following publications:

Sarraceniaceae, by John M. Macfarlane. Engler's Pflanzenreich, vol. iv. 110, 1908.

The American pitcher-plants, by Roland M. Harper. Journal of the Elisha Mitchell Scientific Society, vol. 34, p. 110, 1918.

The biochemistry of the American pitcher-plants, by Joseph S. Hepburn, Frank M. Jones, and Elizabeth Q. St. John. Transactions of the Wagner Free Institute of Science, vol. 11, 1927.

Four articles relating to pitcherplants have previously been published by the writer:

Acidity relations of the *Sarracenias*. Journal of the Washington Academy of Sciences, vol. 19, p. 379, 1929. (The species ranges given in that paper are somewhat modified in the present one in accordance with data subsequently obtained.)

The geographic relations of *Sarracenia purpurea*. The Appalachian relative of *Sarracenia flava*. Bartonia, vol. 15, p. 1, 1933.

Exploring for plants in the Southeastern States. Scientific Monthly, vol. 38, p. 80, 1934.

As pointed out in the paper by the writer on *Sarracenia purpurea*, some recently published maps of the distribution of the members of the *Sarraceniaceae* (Die Pflanzenareale, vol. 3, pt. 1, 1931) are not satisfactory, having been constructed from incomplete data for most of the species. A new set of maps is accordingly presented herewith, based on a thorough review of the literature, a cataloging of numerous herbarium records, and extensive field observations.

The base map shows, in addition to State boundaries, two geologic lines of plant-geographic significance. The more northern of these represents the limit reached by the last, or Wisconsin, ice sheet, as mapped by Antevs (Bulletin of the Geological Society of America, vol. 40, p. 631, 1929). The southern line is the fall line, taken from the map of Physiographic Divisions of the United States, published by Fenneman (Annals of the Association of American Geographers, vol. 6, p. 19, 1917). Most of the territory enclosed between these lines has been continuously available for occupancy by plants since Cretaceous time, when the development of our modern flora began.

On the individual maps, areas where the species is frequent in favorable habitats are dotted. When the boundaries have been fairly definitely determined, they are marked by solid lines, and when only approximately known, by dash lines. Presumable migration routes are indicated by arrows.

Before the individual species are discussed, the geologic relations of the group as a whole require brief consideration. Physiographic studies indicate that prior to and during the Cretaceous much of eastern North America was reduced to a peneplain. The sea then extended up to what is now the fall line, and for some distance northward and westward from this boundary the conditions for plant growth were similar to those of our present-day Coastal Plain. There were vast level areas covered by alluvial sands and clays, traversed by sluggish,

meandering streams, and dotted with bogs and swamps. This was the ancestral home of many present-day species of plants.

During the Tertiary, uplift of the land took place, and erosion developed the present topography. Some of the plants adapted themselves to the cooler climate of more elevated areas and grew there throughout the course of the development of our Blue Ridge and Appalachian Mountains. Others proved unable to adjust their temperature requirements and died out from their ancestral regions. Meanwhile, however, the sea was gradually retreating, leaving land open to occupation by plants, and seeds or other disseminules of many species found their way down various river valleys and developed colonies on the newly formed Coastal Plain. Most of the *Sarracenia*s evidently migrated in this manner.

## CALIFORNIA PITCHERPLANT

*Chrysamphora californica* (Torrey) Greene

Though currently believed to be restricted to a few mountain bogs in California and southern Oregon, a study of the literature and of herbarium records has revealed that California pitcherplant grows in numerous localities from Placer County, California, where it reaches an altitude of over 8,000 feet, to Lane County, Oregon, where the writer has collected it at sea level. It grows in swamps, bogs, and springy places where the reaction is usually intensely acid and the soil temperature probably never exceeds 65° Fahrenheit.

This plant evidently developed, during Cretaceous times, so far west that when the Tertiary uplifts occurred, its seeds failed to reach the drainage basins of any of the eastern rivers, and it accordingly did not colonize the Atlantic Coastal Plain. Instead it migrated westward, and occupied the area which subsequently became the Sierra Nevada and the Coast Ranges, between latitude 39° and 44° N. All traces of the connecting links between this and the related genera *Heliamphora* and *Sarracenia* were destroyed by the geologic events of Tertiary times, or by the advances of the ice sheets of the glacial epoch.





FIGURE I

Distribution of green pitcherplant, *Sarracenia oreophila*



## GREEN PITCHERPLANT

*Sarracenia oreophila* (Kearney) Wherry

Green pitcherplant, the most primitive of the eastern species, was apparently first collected along the inner margin of the coastal plain in Taylor County, Georgia, but it later proved to occur chiefly in the Appalachian Mountains region of northeastern Alabama. It has been found thus far in a number of stream valleys in Cherokee, De Kalb, Jackson, and Marshall Counties, and may be considerably more widespread.\* Unlike most species, it grows in alluvial sands and gravels on stream banks, rather than in bogs or swamps. The soil reaction, however, is rather intensely acid.

In Alabama the Cretaceous peneplain was not uplifted high enough above sea level for the climate to become very much cooler, so that little increase in hardiness was necessary to enable plants to survive there. The ancestral home of this pitcherplant may accordingly be inferred to have been essentially where it now occurs. Of all the species, it has been the least successful in colonizing the Coastal Plain, its seeds having apparently reached that province only after it had become too conservative to spread there.

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\* While this article was in page proof, and after the map was engraved, an additional station for it was discovered in Elmore County, in central Alabama.



FIGURE 2  
Distribution of pale pitcherplant, *Sarracenia sledgei*

## PALE PITCHERPLANT

*Sarracenia sledgei* Macfarlane

The ancestral home of pale pitcherplant was presumably in what is now the Cumberland Plateau of Tennessee, where one or two colonies are reported to survive. It migrated down the Tennessee and the Mississippi River systems, after they developed. Becoming colonized on the Coastal Plain, it then spread eastward into Alabama, there approaching but apparently not intermingling with its eastern relative, *Sarracenia flava*.

It also spread westward across Louisiana and is the only species known to have reached Texas. The westernmost station from which a specimen has been seen is near Athens, Henderson County, nearly at longitude 96° W. There are credible records of this pitcherplant from a short distance farther west, but, growing as it does in acid swamps and springy meadows, it is unable to enter the more arid portions of Texas, and reports of its occurrence there have proved to be erroneous.

The map here reproduced shows the range of this plant as at present known, although it probably grows farther north in the Mississippi Valley and has merely failed to be collected by the few botanists who have explored that region.





FIGURE 3

Distribution of yellow pitcherplant, *Sarracenia flava*

## YELLOW PITCHERPLANT

*Sarracenia flava* Linnaeus

The yellow pitcherplant developed farther east than its relative, the pale pitcherplant, and in the course of the Tertiary uplift and erosion which resulted in the development of the southern highlands it managed to survive in a number of places in North Carolina. As the sea gradually withdrew from the old shore line, leaving new land open for occupation by plants, the seeds of this species traveled down various river systems in North and South Carolina and Georgia, and started colonies in the Coastal Plain. Lateral spreading from these colonies also occurred, and the species reached on the one hand, nearly to the Alabama River, and on the other, to the James River in Virginia.

Like most plants with such a geologic history, this pitcherplant gradually lost its aggressiveness, and by middle Tertiary time its colonies apparently ceased to expand further. Accordingly, although it grows in abundance in moist meadows and depressions in pinelands, it has never been able to enter lower peninsular Florida, which emerged from the sea only toward the close of the Tertiary.





FIGURE 4

Distribution of red pitcherplant, *Sarracenia jonesii*

## RED PITCHERPLANT

*Sarracenia jonesii* Wherry

Red pitcherplant grows mostly in swamps and meadows underlain by loamy soil of moderate or sometimes intense acidity. It seems to have developed in the same general region as *Sarracenia flava*, but somewhat farther north. When the Tertiary uplift took place, this plant managed to survive in a small area in Buncombe and Henderson Counties, North Carolina. Seeds from these colonies never reached rivers flowing into the Atlantic, however, and it failed to migrate in that direction.

Toward the western end of its ancestral area, on the other hand, these relations were reversed. The geologic changes exterminated it from this portion of the range, but before that occurred, seeds reached the headwaters of the Alabama River system, and developed colonies farther down stream. It managed to get a foothold in the Alabama Piedmont province and, when the Coastal Plain emerged from the sea, also invaded that region. Some lateral spreading from the main river valley occurred, so that it migrated a short distance into Florida and Mississippi, but by mid-Tertiary time it had apparently lost all ability to increase its range further.



FIGURE 5

Distribution of whitetop pitcherplant, *Sarracenia drummondii*



## WHITETOP PITCHERPLANT

*Sarracenia drummondii* Croom

The evolutionary changes which resulted in the development of the showy red-flowered *Sarracenia jonesii* from a rather inconspicuous green-flowered ancestor did not come to an end with that species, but continued along several lines. The tendency toward increased size and coloration reached a culmination in whitetop pitcherplant, the showiest of our species. The common name selected for it refers to the predominance of white in the hood.

Development of this pitcherplant evidently took place somewhere in the headwaters of the Alabama River system. The Tertiary mountain-making exterminated it from its ancestral home, but seeds traveled downstream and soon colonized the Coastal Plain. Spreading laterally from this river valley, it migrated a short distance westward into Mississippi and somewhat farther toward the east, into the western extension of Florida. It also formed two isolated colonies, one in Madison County, Florida, the other in Sumter County, Georgia. Reports of its occurrence farther northeast seem to be based on misidentification of other species.



FIGURE 6

Distribution of sweet pitcherplant, *Sarracenia rubra*

## SWEET PITCHERPLANT

*Sarracenia rubra* Walter

As shown by the accompanying map, sweet pitcherplant occurs mostly near the fall line in Georgia and South Carolina, although in North Carolina it extends to the coast. Its northernmost known station is at Southern Pines, in Moore County. There is also an apparently isolated area in western Florida.

This distribution indicates that the species originated, as a descendant of *Sarracenia jonesii*, somewhere on the headwaters of the Santee River system. Being very sensitive to cold, it was exterminated in its ancestral home by the climatic changes accompanying the Tertiary uplift, but seeds meanwhile drifted downstream and colonized the Coastal Plain. Its development chiefly near the fall line indicates its early arrival after the retreat of the sea, but it soon lost its aggressiveness and only locally reached the outer part of the Coastal Plain.

The favorite habitat of the sweet pitcherplant is a moist, grassy thicket near the margin of a swamp, although it can grow also in dense shade. The soil is usually peaty and intensely acid.





FIGURE 7

Distribution of hooded pitcherplant, *Sarracenia minor*

## HOODED PITCHERPLANT

*Sarracenia minor* Walter

Peninsular Florida emerged from the sea only toward the close of the Tertiary age, and as by that time most of the *Sarracenias* had apparently lost their ability to colonize new territory, they are not to be looked for in that region. The one exception to this rule is the hooded pitcherplant, which extends far southward over the State, being reported even in Palm Beach County, at latitude  $26^{\circ}$  N. In other directions its range is more restricted, however; it is the only species which has, so far as known, failed to reach the State of Alabama. It is frequent in southern Georgia, but gradually diminishes in abundance northeastward and barely enters North Carolina.

Such a distribution indicates that the species originated on that part of the Cretaceous peneplain which has since become the Georgia Piedmont. Although unable to survive the geologic changes there, its seeds found their way down the Altamaha River system, and colonized the Coastal Plain. It thrives best in moist meadows or open pinelands, underlain by loamy but intensely acid soil, and as such habitats are common, it has attained a wide range.



FIGURE 8

Distribution of parrot pitcherplant, *Sarracenia psittacina*



## PARROT PITCHERPLANT

*Sarracenia psittacina* Michaux

The distribution indicated on the accompanying map shows that the parrot pitcherplant originated at some point in the ancient peneplain near what is now the northwestern corner of Georgia. From this region it disappeared as a result of the geologic and climatic changes, but its seeds found their way down both the Alabama and Chattahoochee Valleys. The colonies thereby formed on the Coastal Plain expanded laterally, reaching the vicinity of New Orleans on the west and the coast of Georgia on the east. Search for it near Augusta, Georgia, where it was stated by Michaux to occur, has proved unsuccessful, the northeasternmost colony thus far found lying 10 miles southwest of Millen, in Jenkins County.

Like most of the others, this species apparently lost the ability to expand its range farther before the end of the Tertiary. It thrives best in low meadows subject to frequent inundation by acid waters from nearby swamps, but in spite of the abundance of such habitats which developed in peninsular Florida after it emerged from the sea, the plant has never succeeded in entering that region.



FIGURE 9

Distribution of southern pitcherplant, *Sarracenia purpurea venosa*

## SOUTHERN PITCHERPLANT

*Sarracenia purpurea venosa* (Rafinesque) Wherry

Southern pitcherplant occurs in swamps, bogs, and wet meadows in nearly every part of the State of North Carolina. It probably originated in the region now constituting Henderson and adjacent counties, but when this territory was uplifted, the immediate ancestors of the plant were exterminated. There can be little doubt, however, that it is a remote descendant from *Sarracenia jonesii*, which has managed to survive in the same general region, for the flowers of the two are almost identical, in spite of the dissimilar leaf shape.

In the course of time its seeds were transported down several of the eastward-flowing rivers, forming colonies on the Piedmont and ultimately on the newly emerging Coastal Plain. Some seeds also found their way down the Chattahoochee River system, and an extensive series of colonies developed near the coast on either side of this valley. In addition, unlike other species, it migrated from northeastern North Carolina to southern New Jersey, over a strip of land which apparently connected these States during Tertiary and early glacial times.





FIGURE 10  
Distribution of northern pitcherplant, *Sarracenia purpurea gibbosa*

## NORTHERN PITCHERPLANT

*Sarracenia purpurea gibbosa* (Rafinesque) Wherry

Northern pitcherplant ranges from Maryland, Delaware, and New Jersey northward over a vast territory in this country and Canada. The geographic relations, together with the presence of intermediates between the northern and southern subspecies in southern New Jersey, indicate that the northern one originated in that region. Evidently the southern ancestor, after arriving in New Jersey, became variable, and gave rise to descendants differing more or less in morphological and physiological characters. Most of these, lacking ability to extend their ranges, have remained where they originated. One, however, became highly aggressive, and as it also differs in pitcher shape, it is classed as a distinct subspecies.

During the ice advances of the glacial epoch this pitcherplant was of course unable to migrate northward, and merely spread a short distance into Maryland and southern Pennsylvania, but after the retreat of the last ice sheet it soon occupied the newly developed bogs, and even managed to reach sub-Arctic Canada.



## PITCHERPLANTS AND THEIR INSECT ASSOCIATES

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### VICTIMS OF THE PLANTS

That the pitcherplants are "intended" as insect traps—that their capture of insects is not an accident of evolution and of no real significance to the plants—is attested by a mass of evidence which in its entirety is overwhelming. Some of that evidence will be presented here.

The pitched leaves, so flowerlike in coloration and shape that the nonbotanical observer usually mistakes them for true flowers and often compares them with jack-in-the-pulpit or with the spathes of the skunkcabbage, bear out an interpretation that their function, like that of flowers, is the attraction of insects. Confirming that interpretation, these flowerlike pitchers at their more active period diffuse a fruity or honeylike fragrance from a nectar secretion containing fruit sugar, whose attraction for insects is often visibly evidenced by columns of ants climbing their walls and feeding in rows upon the exuding nectar, or by wasps, bees, butterflies, and moths flying from pitcher to pitcher, alighting and feeding upon the nectar globules that stud their tops. The nectar glands are so distributed that they form attractive pathways for the visiting insects, which are further guided by bristly hairs or by a fine pile, so directed that a feeding insect is unconsciously urged toward and into the pitcher's mouth. Within the mouth of the pitcher the surface texture changes to one of extreme smoothness, as a result of which the visiting insect is precipitated to the bottom of the pitcher. From this detentive area escape is rendered difficult by steep and narrow walls, smooth or lined with downward-directed hairs; often, too, the falling insect is plunged into a liquid which fills the lower portion of the pitcher's tube and which has the property of quickly terminating the struggles of an entrapped insect, so that within a few seconds all efforts toward escape cease, and rarely does even the strongest insect succeed in gnawing its way out through the pitcher's walls.

This pitcher liquid, originally a natural secretion of the plant, but eventually more or less contaminated and diluted from outside, is thus an important part of the insect trap. Its continued effectiveness is enhanced by its rapid increase in volume in response to the presence of nutrient matter; that is, the liquid increases in quantity as insects are captured, and experimentally, to a surprising degree, when milk or raw meat, for example, is introduced into a pitcher. In most species the pitcher liquor contains a proteolytic enzyme, similar in its properties to the digestive enzymes of the mammalian stomach; steeped in this stupefying and digestive liquid, the softer parts of the entrapped insects are quickly dissolved. Absorption by the plant from the fluid contents of the pitcher has been demonstrated by careful experiment and chemical study.

Added to the cumulative evidence of these characters of the pitcherplants and other



characters possessed by individual species among them but not common to the group—characters which taken together are susceptible of the single interpretation that they are adaptations or adjustments for the capture and utilization of insects by the plants—there is the further evidence that as insect traps they are astonishingly effective—that as traps, they work.

Of all our pitcherplants, perhaps *Sarracenia purpurea* and *Sarracenia psittacina* are comparatively the least successful as insect traps. The sphagnum-embedded pitchers of *purpurea*, however, functioning as water-filled pitfalls for attracted insects, or for those casually wandering by, usually contain a few insects in their lower tubes, and sometimes they are crammed with the bodies of beetles, crickets, or grasshoppers, when these insects abound. Although the narrow-entranced pitchers of *psittacina*, may reveal little evidence, beyond an occasional spider, of numerous captures, they are sometimes (and especially after the subsidence of temporary floodwaters which have covered low-growing plants) literally stuffed with the polished bodies of water beetles, held rigidly by the long elastic hairs which line the narrow tubes.

Although the hooded pitchers of *Sarracenia minor*, and the slender grouped pitchers of *S. rubra* capture a wide range of insect species, yet these plants seem to specialize in the capture of ants, big and little, and their pitchers are often packed for several inches of their length with the bodies of hundreds of ants, sometimes of a single abundant species from some adjacent anthill.

Of the larger pitcherplants such as *S. flava*, *sledgei*, and *drummondii*, only those who have walked through expanses of their tall pitchers, lifting their hoods and peering in at their more recent captures, occasionally splitting open a mature pitcher and investigating its varied contents, can appreciate the enormous number and variety of these captures, even in surroundings which are not otherwise obviously rich in insect life. Here the entomologist may find many species: beetles, large and small, bees, wasps, parasitic Hymenoptera, moths, flies, grasshoppers, even such actively flying insects as butterflies and dragonflies, and including species whose local presence he may not have even suspected. Spiders, living and dead, are frequent occupants. Not rarely, little green tree toads sit by day within the mouths of the larger pitchers; but their bones, and those of the slender “chameleon” lizards, embedded among the fragmentary insect remains below, bear witness to the fact that even these vertebrates are not always successful in escaping the trap when once they have ventured within the pitcher’s mouth.

Similarly, the pitchers of *Chrysamphora* (*Darlingtonia*), from the first hours of the opening of their cobra-like hoods, begin to capture insects, until their great tubes are stuffed with insect remains, which in variety form almost a cross-section of the insect fauna of the plant habitat. This western species seems to lack the digestive enzyme of *Sarracenia*, and soon its accumulated insect captures are converted into an ill-smelling mass, even contaminating the air of their mountain bogs with the odor of decay.

The pitcherplants are real insect traps.



## POLLINIZERS

Pitcherplants, by their trap structure almost unique in their relations to the insect world, do not confine those relationships to the status of trap and victim. The flowers of *Sarracenia* are dependent upon insects for their pollination, and they are adjusted structurally and physiologically to encourage, if not to enforce, cross-fertilization by insect agency.

For example, the globular flowerbud of *Sarracenia flava*, in March or April, pushing up rapidly from its fleshy rootstock, is at first held upright upon its stem; but before the swelling bud has lost its globular form, it makes a complete reversal of position, so that when the petals expand the flower opens downward. The promptly shed pollen falls into the concavity of the umbrella-shaped style which closes the flower below. The stigmatic points are entirely outside the dome-shaped cavity formed by the petals and having the style as its floor; for they are located, one at each of the five projecting points of the umbrella. A visiting insect, alighting on the shelflike base of a petal, turns either right or left to an opening between two adjacent petals and under one of these points, against which (if the insect should be of suitable size) it scrapes its pollen-dusted back as it enters. On departure, the insect may leave the flower by the same route; but especially in the more loosely textured flowers of other species, escape is readily and more frequently made at some other point around the edge of the umbrella.

Though the pollen is shed promptly after the opening of the flower, nectar continues to be secreted and insects attracted for many days, even for several weeks, after that event; and a further change in the position of the flower (this time toward the vertical) commences within a day or two of its opening, thus tending to spill out the pollen and to permit visiting insects to avoid intimate contact with that which may have accumulated in the concavity of the style. These phenomena bear out the interpretation that in *Sarracenia* the fall of the pollen is antecedent to the receptivity of the stigmas of an individual flower, and that fertilization is effected by an entering insect which has received its pollen-coating in another flower.

Ants, bees, and pollen-eating beetles are all frequent visitors to the flowers of *Sarracenia*. Among their visitors, thick-bodied bumblebees can scarcely force an entrance between the petals without scraping one of the stigmatic points; the *Sarracenia* flies frequently crowd into the blossoms, apparently more for shelter at night and in bad weather than in search of food; honeybees are regular visitors, and they more nearly fit the entrances than do the smaller wild bees of several species, which, nevertheless, are usually the more numerous among the insect visitors and which are probably the insects most concerned in effecting fertilization. Thus these flowers, attractive to a considerable range of insect species, are not dependent upon any one insect for the transference of their pollen from flower to flower.

## PLANT-EATING INSECTS

The most familiar plant-insect relation is that existing between a foodplant and the insect which attacks it. Several insect species have the *Sarracenia*s as their preferred or their sole food,

under conditions which for them eliminate the danger of the plant's trap structure, which is so generally fatal to other insects. The flowers, and seasonally later the seed vessels of *Sarracenia*, in all its species and apparently throughout its geographical distribution, are eaten by small greenish caterpillars with black heads, which, having completed their work of destruction, spin flimsy cocoons among the refuse of their feeding or for pupation sometimes tunnel into the hollow flower stem, and finally emerge as small dark-colored moths (*Olethreutes daeckiana* or *O. hebesana*), to continue in turn this life cycle of destruction. Being thus concerned only with parts of the plant which do not bring them into contact with the pitcher's trap, without danger to themselves they sometimes destroy a very considerable percentage of that seed which has been made possible by the visits of another set of insects, the pollinizers.

The fleshy, starch-filled rhizomes of all species of *Sarracenia* offer a safe food supply to another and much larger insect, a pale boring caterpillar which attains a length of nearly two inches. It tunnels the rootstocks, pouring out on the ground about the plant many corky pellets, ferruginous in color, thus giving a ready clue to its destructive presence. Sometimes these pellets are built up into a turretlike structure, resembling in miniature the mud turrets of the crayfish. The parent moth of the *Sarracenia* root-borer (*Papaipema appassianata*) is a beautiful creature, maroon-red and yellow in color, and was long so rare that only a single specimen was known in all the museums of the world; but since the discovery of its pitcher-plant habitat, entomologists have been able to procure specimens in any desired number. The moth emerges in the early autumn and deposits its seedlike eggs; in the spring the eggs hatch as little boring caterpillars, which tunnel their way into the rootstock, with an entrance at the terminal bud. Like the related and too familiar iris borer, this insect sometimes survives the transportation of the plants even to foreign countries, destroying plants which may have been procured at great trouble and expense.

Because of its habits, the *Sarracenia* root-borer does not of necessity come into conflict with the pitcher's trap. There are, however, three other insects having *Sarracenia* as their obligatory foodplant (for they will eat nothing else), which are concerned, not with blossom or seed or root, but with the pitchers themselves. They are the three pitcherplant moths, which throughout their lives, from egg to adult, are in intimate contact with the pitchers, at every turn and change of their varied existence utilizing these dangerous structures to their own advantage.

The pitcherplant moth sits in a pitcher, head up, throughout the day. If disturbed, it backs further down the narrowing tube; and if compelled to fly out, it flies rapidly to another pitcher, near or far, alights outside, and runs in over the rim, where once more it assumes the habitual head-up position upon the pitcher's inner wall. This ability to enter and leave the pitcher trap seems to consist simply in knowing how; for the moths do not exhibit any marked structural adaptation to assist them. The three pitcherplant moths all belong to the same genus, *Exyra*; and although each *Exyra* species is able to survive for a time in association with any *Sarracenia* species, yet they do exhibit some habitual preferences among these plants.



One of these *Exyras*, *rolandiana*, is consistently associated with *Sarracenia purpurea* throughout much of that plant's wide geographical range. Wine-red, yellow, and smoky purple in color, this moth matches well the highly colored walls of the open-topped pitcher in which it sits by day. The other two *Exyras*, *semicrocea* and *ridingsii*, are not found north of Virginia; they retain their (probably) ancestral colors of dull yellow contrasted with smoky black, and they are habitually associated with those other *Sarracenias* whose hooded or lid-covered pitchers offer better concealment from outside view, so that color for these moths may not have the same significance.

The moths lay their minute eggs on the inner walls of the pitchers. Hatching from these, the little caterpillars, throughout life and by various devices, maintain for themselves closed feeding chambers, in which they may live with some degree of concealment and protection from external foes. This they accomplish by closing the mouth of the pitcher above, and by feeding below only on the inner layers of the pitcher's wall, until this is reduced to a bladderlike thinness, the caterpillar as it feeds sealing all accidental holes and fissures with silk. To close the pitcher's mouth, one of several alternative methods is employed. The more prevalent of these is to spin a fine, close, and almost opaque web across the throat of the pitcher; or in a young and tender pitcher, a tightly closed chamber is often attained by eating a threadlike groove encircling the upper portion, above which groove the pitcher dies, dries, and hardens, thus effectually and permanently closing the pitcher at the top. One or the other of these methods is usually followed, either to obtain a closed feeding chamber with its added safety, to provide a retreat for pupation, or in the autumn to prepare a hibernaculum for the young larva, which must survive the winter in that concealment; for thus all the *Exyras* pass the winter, each ensconced in a pitcher of *Sarracenia*.

The young larva of *semicrocea*, when it finds itself in the narrow-throated pitcher of *psittacina*, varies this method by closing the pitcher's constricted throat with a dense wad of chewed vegetable fragments and silk, ensuring for itself a watertight compartment for the winter; and *ridingsii*, in its larger pitcher, constructs a vaulted chamber among the refuse of its own feeding.

When about to pupate in a web-ceiled pitcher, the caterpillar of *Exyra* makes no provision for the exit of the moth, which by slight pressure from within is able to force a way through the thin web; but in the narrow-throated pitchers of *psittacina*, or in the purposefully collapsed pitchers of *flava*, the larva, before spinning its cocoon, cuts a small round hole in the pitcher's wall as a provision for the emergence of the moth to be, which would otherwise be unable to find or force its way out to the open air.

These and other adjustments of *Exyra* to life within the pitchers of *Sarracenia* are in the main psychical rather than structural; but in various stages of their existence structural modifications, too, seem to relate to life within the pitchers. In illustration, along the bodies of the caterpillars of the two *Exyras* which live in the narrow-tubed southern *Sarracenias* are several strongly spined elbowlike projections which hold them out from close contact with

the walls of the pitchers and prevent these larvae from being wedged fast in the tapering cavities they inhabit; whereas the caterpillar of *rolandiana*, living in the squat, open-topped pitchers of *purpurea*, does not so greatly need nor does it possess these appendages.

Thus instinctive and structural adjustments make possible a relationship between insect and insect-eating plant, entirely to the plant's disadvantage; and the conclusion seems inevitable, that although the plant has brought its trap structure to such perfection that few insects may escape it, yet the pitcherplant moths, in their evolution, have met these dangerous conditions and have actually turned them to their own advantage.

#### PITCHER ROBBERS

In nature, the usual response to any concentration of potential food supply is a flocking in of claimants for that food; so that it is to be anticipated that the store of animal matter accumulated in the pitchers of *Sarracenia*, when once their traps become operative, should attract other animals, and that some of these should evolve methods of eluding the trap and of securing for themselves a portion of that food. These pitcher robbers are of a number of species, and some of them are so permanently adjusted to life as associates of the pitcherplants that they have lost the ability to survive under any other conditions. For example, no sooner have captured insects begun to accumulate in the pitchers than among the dead and dying insects we may usually find one or several living whitish maggots, which in fluid-filled pitchers wriggle their way up to each fresh capture and commence to feed upon it as it floats on the surface. The larger of these maggots are the young of the *Sarracenia* flies, genus *Sarcophaga*, with at least six species having this habit and habitat. As young maggots, they are deposited within the pitcher's mouth by the parent fly. Feeding upon its captures until they have attained larval maturity and a length of about three-quarters of an inch, they then usually leave the pitcher and change to brown puparia in the sand or moss at the base of the plant. From these puparia in due course emerge adult flies, which continue the life cycle as before.

These insects, throughout their stages, seem to possess no structural adaptations to fit them for life in their dangerous habitat; but like the pitcherplant moths, they know their way in and out of the pitchers and rarely fall victim to the trap. They confer no benefit upon the plant in compensation for their robbery of it, unless the habit of the flies of crowding into the flowers at night and on stormy days may give them status as pollinizers, to which office their appropriate size and their bristly integument seem to fit them. One remarkable character of these larvae may have originated as a needed defense, for like the intestinal worms of mammals, these fly larvae contain an anti-enzyme which inhibits digestion, so perhaps their ability to spend their lives, bathed in the digestive fluids of the pitchers, is attributable to this quality as a necessary defensive character.

*Sarcophaga* larvae are the largest but by no means the only pitcher-robbing insects. No sooner does the cobralike hood of *Chrysamphora* (*Darlingtonia*) expand and its mouth open than the first few insect captures appear in the clear fluid which fills the lower portion of



the tube; and among these almost invariably appear whitish threadlike "worms" which increase in numbers as the captures increase, until a writhing mass of these larvae occupy the bottom of the pitcher, often wriggling up to surround each fresh victim as it floats and struggles above the decaying mass of earlier captures. These larvae, to be found in almost every open and functioning pitcher of the California pitcherplant, were a perpetual puzzle to Mrs. Mary Austin, who sixty years ago spent so many patient hours among these plants in Plumas County and of whom Asa Gray then wrote that she had given us most of our detailed knowledge of these wonderful plants; for Mrs. Austin never detected the frail little gnat, *Metriocnemus edwardsi*, smaller than a mosquito, which lays the eggs from which these pitcher-robbing larvae hatch. On the opposite side of our continent, a related and very similar gnat (*Metriocnemus knabi*) is the parent of larvae which live in and rob the water-filled pitchers of *Sarracenia purpurea*, wherever this plant grows.

In these same water-filled pitchers of *purpurea* live the "wrigglers" of the pitcherplant mosquito, *Wyeomyia smithii*. Even in midwinter, when the pitchers' contents have been frozen to solid cores of ice, these larvae are there, ready to resume activity and to complete their transformations with the coming of spring. This little mosquito, harmless to human beings and representative of a tropical genus, yet extends its range well over the Canadian border, and rarely is it absent from any considerable colony of this pitcherplant species, which constitutes its only home.

In the drier pitchers of other species, the larger black-headed larvae of another fly may often be seen hollowing out the bodies of the captured insects and eventually constructing frail frothlike cocoons among these remains. This insect has been named *Sciara macfarlanei* in honor of Dr. John M. Macfarlane, the monographer of the pitcherplants of the world. With somewhat similar habits, the young of a few other small flies are occasionally to be met with, taking advantage of the store of animal food provided by these plants; but most, if not all, of these are only casually present as scavengers, and not as obligatory associates of the pitcherplants.

#### PITCHER DWELLERS

We have not yet exhausted all possible variations of insect association with these plants; for some species visit or utilize the pitcherplants, not as sources of food supply, but to adapt the pitcher structures to other purposes of their own—usually as shelters for themselves or for their young. The little tree toads, of which mention has already been made, may often be seen sitting within the mouths of the larger pitchers; but since it is the habit of these creatures to seek any small cavity which offers them seclusion for the day, their presence in the pitchers may have no further significance, even though it may permit the occasional capture by them of attracted insects.

Spiders of many species occur in and about the pitchers, and it may be said of one kind that it does sometimes utilize the pitcher's structure. A large Lycosid spider, whose habit it is to carry about and protect its spherical egg sac, sometimes roughly barricades the mouth



of a dry pitcher with coarse cobweb and vegetable litter, and within the cavity thus created, guards its treasured eggs until the hatching of the young.

The petals of *Sarracenia* are often neatly scalloped by a leaf-cutter bee, which occasionally utilizes a dry pitcher for its nest, building therein its series of thimble-shaped cells and storing them with food for its young.

There is one insect, however, which by frequent and habitual use of the pitchers of several species of *Sarracenia*, deserves to be called the *Sarracenia* wasp. This is a slender-waisted black wasp which plugs the lower portion of a pitcher with grass or moss, partitions off a series of cells, provides each in turn with a store of freshly killed grasshoppers or of tree crickets, deposits one of its own eggs in each of the cells, then tops this nest with a densely packed wad of grass or moss, completely closing the pitcher above. The geographical distribution of this wasp is more extensive than that of the pitcherplants it inhabits, so elsewhere it must utilize other cavities; but at least from North Carolina to southern Mississippi, wherever suitable *Sarracenias* abound, they are utilized by this wasp as sites for its nests.

#### ECOLOGICAL COMPLEXITIES

These insect-eating plants, dependent upon insects for their pollination, fed upon in all their parts by other insects, systematically robbed of their captures, dwelt in by other series of insects, would seem to illustrate every imaginable relationship between the plant and animal worlds; but in reality these enumerated relationships present only the framework of further ramifications of conflicting interests, which extend to the vertebrates as well as to the lowlier representatives of the animal world.

By what deterrent qualities are the pitcherplants protected against grazing animals which crop every available mouthful of grass among their conspicuous growths, but which leave the showy pitchers untouched? It was a quaint conceit of Miller (1739) that the water-filled pitchers of *Sarracenia* are providentially provided drinking fountains for thirsty birds; and Catesby interpreted them as safe retreats for insects when endangered by their foes. In reality, birds are sometimes concerned with what goes on within the pitchers: the *Exyra* caterpillar which cuts a drainage hole and an emergence hole in an otherwise closed pitcher in preparation for pupation and the emergence of the moth, by these slight external signs gives notice to sharp-eyed birds that a desirable food-morsel is hidden within; and sometimes, on the pitcherplant meadows of the south, it is difficult to find a pitcher bearing these indications that has not been slit lengthwise by the beak of a searching bird which has learned their significance.

We do not know how many kinds of predators—wasps, spiders, Acarids—habitually prey upon pitcherplant insects; but of parasitic insects which attack them, the number is not small. Even the minute egg of the pitcherplant moth, glued to the pitcher's inner wall often yields, instead of its rightful occupant, a little caterpillar, a motelike parasite; this under the microscope proves to be an unbelievably small wasplike creature complete in all its parts,

wings, legs, eyes, antennae, whose parent must have searched out the minute egg of *Exyra* and whose entire life cycle must have been completed within the eggshell's bounds. Other and larger parasites, some wasplike, some two-winged flies, are fatal to the larvae of *Exyra*, and perhaps the brief exposure of these larvae when occasionally they move from pitcher to pitcher may give opportunity for the parent parasite to deposit its egg on the otherwise well-hidden caterpillar. The larvae of the pitcher-robbing *Sarracenia* flies would seem reasonably safe from parasitic attack; but their brown puparia often yield not flies, but whole flocks of little wasplike parasites which emerge in a procession through holes gnawed in the rigid walls of a puparium. The rootborer, *Papaipema*, also has its parasites. The larvae of the *Sarracenia* wasp in their well-packed cells are not immune; nor are parasites their sole danger; for before the rightful occupant of a cell has had time to consume its store of food, this is often plundered by ants or by other insect scavengers. Ants, too, though among the more frequent victims of the leaf trap, sometimes actually build their nests in a dry pitcher (do they drain it first?), and even construct a paperlike narrow-entranced door across its mouth, excluding other insects. Thus all sorts of complications arise, when insects having conflicting interests attempt to occupy the same pitcher. Not rarely, an *Exyra* caterpillar, closing a pitcher for its own use and thus preventing the entrance of other insects, incidentally starves the *Sarcophaga* larva already ensconced below and dependent upon the entrance of fresh victims for its food.

So, from our observation of the complicated relationships which reveal the pitcherplants as focal points of contact between the plant and animal worlds, emerges a more vivid realization that in nature each plant, each animal species, exists for itself alone; that its whole economy of life relates to its own growth, its own safety, its own specific survival; and that in the attainment of these ends, its environment is not confined to the obviously immanent, but that its expanding circles of influence fade from our view into the distant and the remote.



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